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ON THE CRANIAL MORPHOLOGY OF SCOLECOMORPHUS ULUGURUENSIS (BARBOUR & LOVERIDGE)

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With 12 Text-Figures

(Submitted: October, 1956)

ABSTRACT

The cranial anatomy of *Scolecomorphus uluguruensis* is compared with that of other genera of *Apoda*. The skull shows neotenic features, such as the total absence of the stapes and the persistence of separate nasals, premaxillaries, prefrontals and septomaxillaries. The absence of the quadrato-stapedial articulation and the musculus levator quadrati is probably unique among *Apoda*. The skull is monimostylic and zygokrotaphic.

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INTRODUCTION

The *Apoda* are distributed throughout the tropical parts of the world, with representatives in the Ethiopian, Neotropical and Oriental regions. According to Werner (1931) there are nineteen different genera and more than sixty known species, all belonging to one single family—the *Caeciliidae*.

The genus *Scolecomorphus* was erected by Boulenger (1883), who gave a short description of the Nyasaland species, *Scolecomorphus kirkii*. *Scolecomorphus uluguruensis* was first described by Barbour and Loveridge (1928). This species is confined to East Africa, its chief habitat being, according to Barbour and Loveridge (1928), the rotting leaf-mould in the rain-forest in the Uluguru Mountains of Tanganyika Territory.

Except for the work done by de Villiers (1938), who made a notable contribution to our knowledge of the cranial nerves and bloodvessels associated with the suspensorial region, which he compared with those of another East African species, *Boulengerula boulengeri*, very little is known about this species.

MATERIAL AND TECHNIQUE

Thanks to the courtesy of Mr. Arthur Loveridge of the Museum of Comparative Zoology at Harvard College, two specimens of *Scolecomorphus uluguruensis* were placed at my disposal. The heads of these specimens were prepared for microtomy in the usual way. They were bulk-stained in borax-carmine, cut at a thickness of 15μ and counterstained in Azan solution. The head of the 26·5 cm. specimen was sectioned transversely and that of the 27·5 cm. one sagittally. A small slab of liver embedded with each specimen provided a fairly reliable baseline, which is an essential for accurate reconstructions. The graphic reconstructions were made according to the method devised by Pusey (1939). A wax model proved extremely useful in the study of the general topography of the skull.

OLFACTORY ORGAN

The olfactory organ and its associated structures have been fully described in *Ichthyophis glutinosus* (Wiedersheim, 1879 and P. and F. Sarasin, 1890) and *Siphonops* and *Coecilia* (Wiedersheim, 1879). The olfactory organ of *Scolecomorphus* does not deviate significantly from that of the above species.

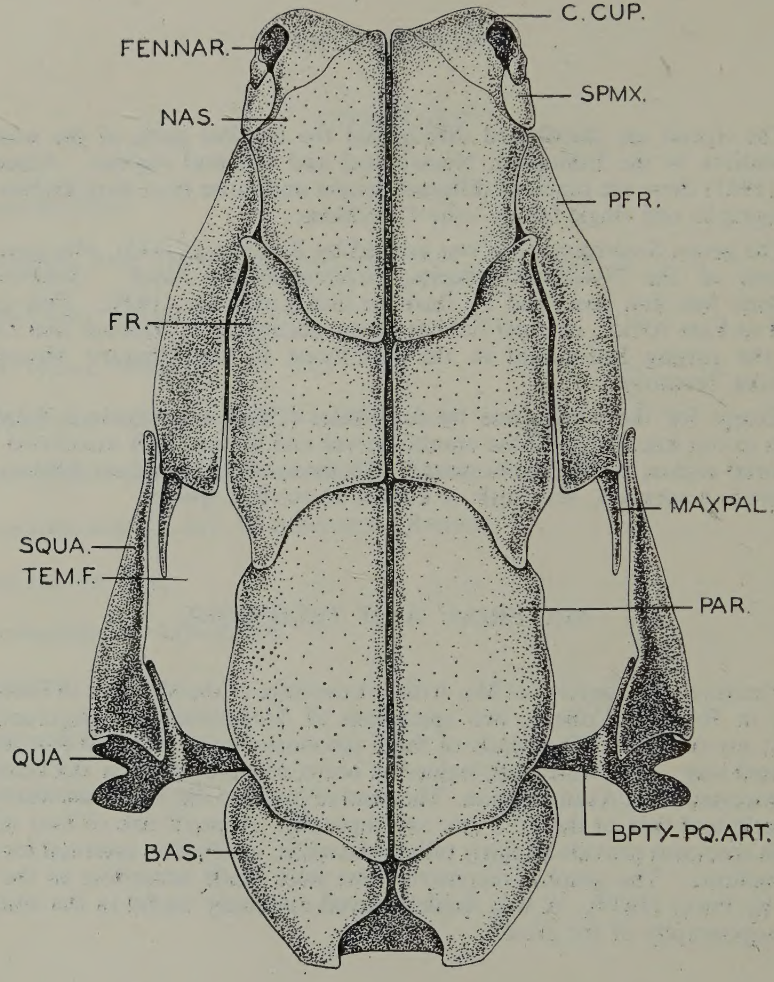

FIG. 1.

Graphic reconstruction of skull × 22·2. Dorsal view.
BAS., basal bone; BTY-PQ. ART., basipterygoid-palatoquadrate articulation; C. CUP., cartilago cupularis; FEN.NAR., fenestra narina; FR., frontal; MAXPAL., maxillopalatine; NAS., nasal; PAR., parietal; PFR., prefrontal; QUA., quadrate; SPMX., septomaxillary; SQUA., squamosal; TEM. F., temporal fossa.

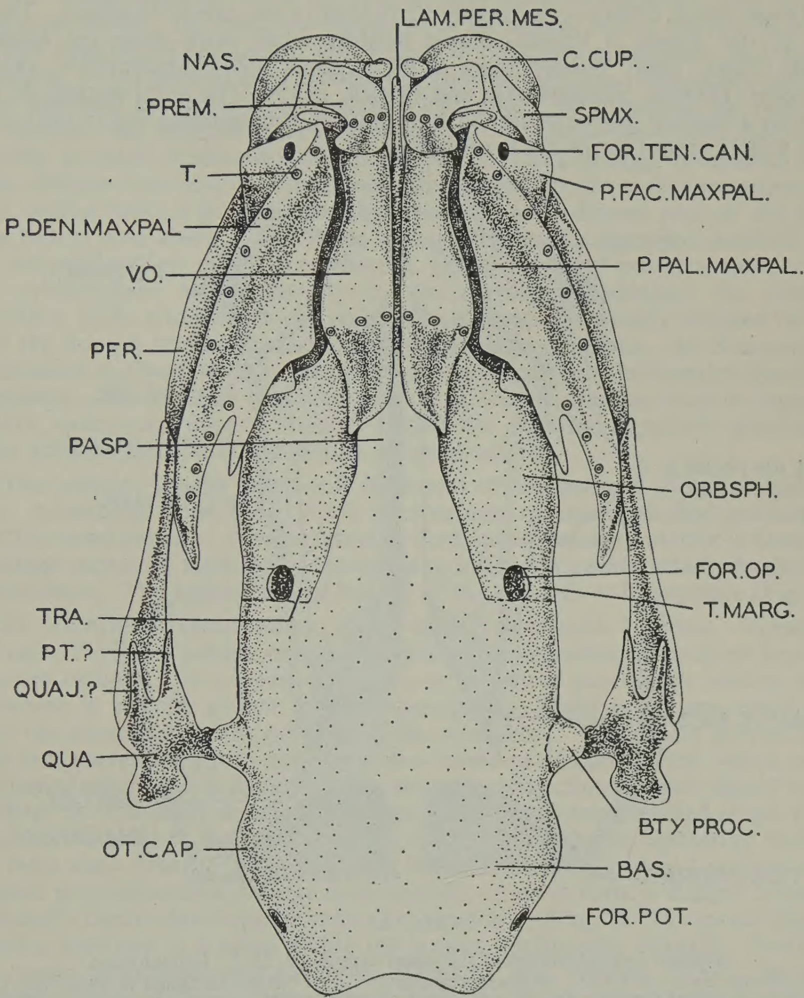

FIG. 2.

Graphic reconstruction of skull × 22·2. Ventral view.

BAS., basal bone; BTY.PROC., basipterygoid process; C.CUP., cartilago cupularis; FOR.OP., foramen opticum; FOR.POT., foramen postoticum; FOR. TEN.CAN., foramen for tentacle canal; LAM.PER.MES., lamina perpendicularis of the mesethmoid; NAS., nasal; ORBSPH., orbitosphenoid; OT.CAP., otic capsule; PASP., parasphenoid; P.DEN.MAXPAL., pars dentalis of the maxillopalatine; P.FAC.MAXPAL., pars facialis of the maxillopalatine; P.PAL.MAXPAL., pars palatina of the maxillopalatine; PREM., premaxillary; PFR., prefrontal; PT., pterygoid; QUA., quadrate; OUAJ., quadratojugal; SPMX., septomaxillary; T.MARG., taenia marginalis; T., tooth; TRA., trabecula; VO., vomer.

The resorbtion of certain cartilaginous structures has resulted in a nasal capsule in the *Apoda* which differs considerably from that of the other *Amphibia*. The nasal capsule of the *Apoda* is known almost entirely from work done on *Ichthyophis glutinosus* (Peter, 1898; Wiedersheim, 1879; Higgens, 1920; Stadtmüller, 1936) and *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935). The nasal capsule of *Ichthyophis* shows a marked degree of similarity to that of *Hypogeophis*, but in both of these it differs widely from that of *Scolecomorphus*.

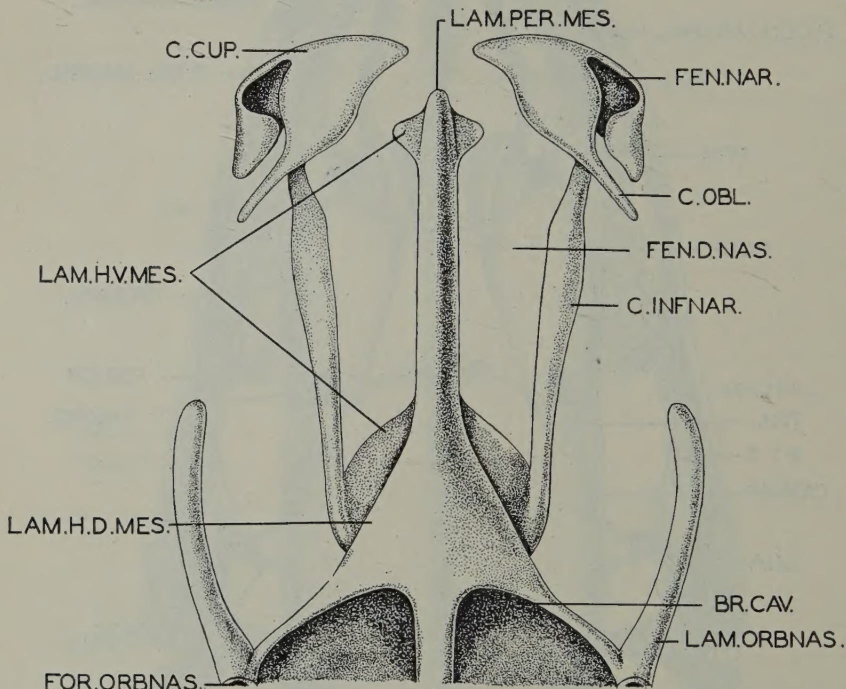

FIG. 3.

Graphic reconstruction of the nasal capsule × 33·3. Dorsal view.
BR.CAV., Brain cavity; C.CUP., cartilago cupularis; C.INFNAR., cartilago infranarina; C.OBL., cartilago obliqua; FEN.D.NAS., fenestra dorsalis nasi; FEN.NAR., fenestra narina; FOR.ORBNAS., foramen orbitonasale; LAM.H.D.MES., lamina horizontalis dorsalis of the mesethmoid; LAM.H.V. MES., lamina horizontalis ventralis of the mesethmoid; LAM.ORBNAS., lamina orbitonasalis; LAM.PER.MES., lamina perpendicularis of the mesethmoid.

Anterior to the fenestra narina, the nasal capsule is more or less dome-shaped (Figs. 3 and 4), and its front wall is known as the cartilago cupularis or processus alaris (Stadtmüller, 1936). The fenestra narina is situated dorso-laterally and is bounded anteriorly, laterally and postero-laterally by the cartilago cupularis and medially by the cartilago obliqua. The cartilago infranarina which is confluent with the ventral portion of the cartilago cupularis stretches backwards and fuses with the lamina

horizontalis ventralis of the septum nasi (= lamina perpendicularis of the mesethmoid, Marcus, Stimmelmayr and Porsch, 1935) (Figs. 3 and 4). The shape of the cartilago infranarina is also responsible for the ventral indentation of the main nasal sac, giving it a semilunar shape. The mucous membrane of the lateral half of the lateral arm consists of low respiratory epithelium and the rest of olfactory epithelium. In *Ichthyophis* (Stadtmüller, 1936) the cartilago infranarina and the cartilago obliqua are continuous with the side-wall or processus antorbitalis (= lamina orbitonasalis, de Beer, 1937), which borders the fenestra narina posteriorly. In *Scolecomorphus*, however, an appreciable amount of reduction has taken place. The cartilago infranarina and the cartilago obliqua have lost continuity with the lamina orbitonasalis; consequently the fenestra narina lacks a posterior border and the antero-lateral part of the fenestra dorsalis nasi is also absent. The latter is very large and is bounded medially by the lamina perpendicularis of the mesethmoid, posteriorly and postero-laterally by the lamina orbitonasalis and anteriorly by the cartilago cupularis. In *Ichthyophis* (Stadtmüller, 1936) a median dorsal connexion is present anteriorly between the dorsal edge of the lamina perpendicularis and the cartilago cupularis. In *Scolecomorphus* this connexion is absent so that the antero-medial border of the fenestra dorsalis nasi is incomplete. The absence of this connexion in *Scolecomorphus* must be regarded as secondary, since, according to Higgens (1920), the cartilago cupularis arises laterally from the anterior portion of the lamina perpendicularis.

The fenestra basalis anterior is large and of no apparent morphological significance. According to de Beer (1937), it represents an unchondrified portion of the floor of the nasal capsule. Antero-laterally the fenestra basalis anterior is bounded by the cartilago cupularis, laterally by the cartilago infranarina and medially by the lamina perpendicularis. The antero-medial border of the foramen is incomplete (Fig. 4).

In *Ichthyophis* (Stadtmüller, 1936) and *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935) the lamina perpendicularis of the mesethmoid projects beyond the cartilagines cupulares as a median rostrum or processus praenasalis medius inferior. This process is entirely absent in *Scolecomorphus*. There is no internasal septum between the extreme anterior portions of the nasal sacs. The lamina perpendicularis appears in transverse sections anteriorly as a round cartilaginous rod, which occupies the internasal cavity and is flanked by the ventrally projecting anterior tips of the nasal bones (Fig. 5). Caudally the lamina perpendicularis becomes ossified (Figs. 6 and 8) and extends dorsally to the upper margin of the nasal organs, separating them completely from each other (Fig. 6). Farther backwards the dorsal and ventral parts of the lamina perpendicularis enlarge considerably, so as to form a lamina horizontalis dorsalis and a lamina horizontalis ventralis respectively (Fig. 7). The ramus dorsalis n. olfactorii is enclosed in a canal within the lamina horizontalis dorsalis. Similar conditions occur in *Hypogeophis* (Marcus, Winsauer and Hueber, 1933). Posteriorly the lamina perpendicularis is continuous with the lamina praecerebralis or lamina cribrosa (Wiedersheim, 1879). The latter consists of a transversely disposed bony lamella, which separates the nasal cavity from the brain cavity. The lamina orbitonasalis arises from the antero-lateral aspect of the lamina praecerebralis. The orbitonasal foramen transmitting the nasal branch of the profundus nerve, is situated between the lamina praecerebralis and the lamina orbitonasalis (Fig. 3). In *Ichthyophis* the lateral branch of this nerve, soon after entering the nasal capsule, emerges through the foramen epiphaniale situated postero-laterally in the lamina orbitonasalis, while the n. medialis nasi V(*a*) runs by the side of the lamina perpendicularis and emerges through the foramen apicale, which is situated antero-medially in the cartilago cupularis. In *Scolecomorphus* the foramen apicale is absent and the n. medialis V(*a*)

leaves the nasal capsule through the fenestra dorsalis nasi and enters a canal within the nasal bone. A foramen epiphaniale is also absent and the n. lateralis nasi V(*a*) leaves through the incomplete side-wall of the capsule.

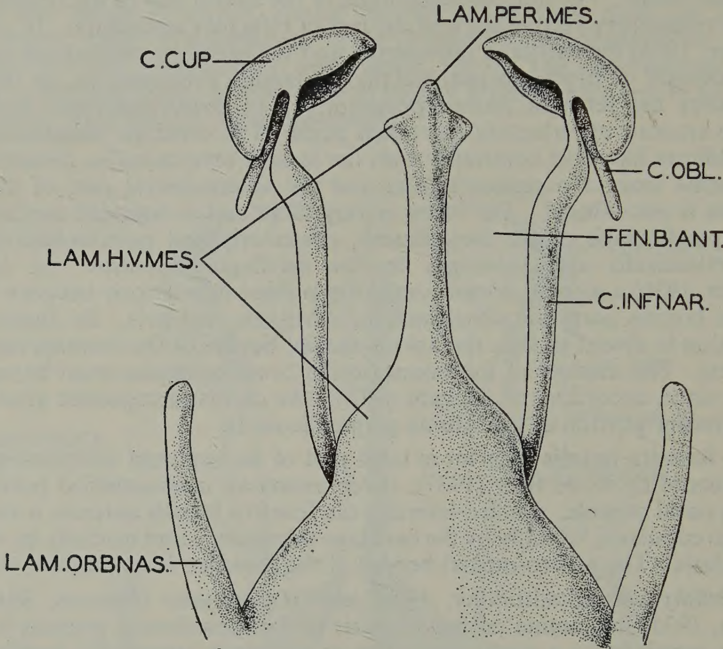

FIG. 4.

Graphic reconstruction of the nasal capsule × 33·3. Ventral view.
C.CUP., cartilago cupularis; C. INFNAR., cartilago infranarina; C.OBL., cartilago obliqua; FEN.B.ANT., fenestra basalis anterior; LAM.H.V.MES., lamina horizontalis ventralis of the mesethmoid; LAM.ORBNAS., lamina orbitonasalis; LAM.PER.MES., lamina perpendicularis of the mesethmoid.

In *Ichthyophis* (de Beer, 1937) the anterior portion of the lamina orbitonasalis is connected to the lamina perpendicularis (= trabecular plate, de Beer, 1937) by means of a trabecular horn. This connexion constitutes the anterior border of the fenestra choanalis (= fenestra basalis posterior, Stadtmüller, 1936). Posteriorly, in *Ichthyophis*, the side-wall bears a short cartilago ectochoanalis which forms the antero-lateral border of the fenestra choanalis. In *Scolecomorphus* the anterior portion of the lamina orbitonasalis, and consequently also the connexion with the lamina perpendicularis, is absent. It also lacks a cartilago ectochoanalis, with the result that the fenestra choanalis is bounded only by the lamina praecerebralis medially and by the lamina orbitonasalis postero-laterally.

The foramina for the transmission of the olfactory nerves are similar to those of *Ichthyophis* (Stadtmüller, 1936). The nervus olfactorius inferior (= ramus ventralis nervi olfactorii, Marcus, Winsauer and Hueber, 1933) is situated medially in the lamina praecerebralis of the mesethmoid. The nervus olfactorius superior (= ramus dorsalis nervi olfactorii, Marcus, Winsauer and Hueber, 1933) enters the nasal cavity through

the sulcus for the nervi olfactorii superiores, which is situated dorsally in the mesethmoid (Fig. 8). In *Hypogeophis*, however, this sulcus is transformed into a foramen.

MEMBRANE BONES OF THE NASAL REGION

The floor of the cavum nasale is formed by three bones, the premaxillary, the vomer and the maxillopalatine. In *Scolecomorphus*, *Ichthyophis* (P. and F. Sarasin, 1890) and *Uraeotyphlus* (Peters, 1881), the premaxillary is a separate bone and forms the anterior portion of the arch of the upper jaw. In all the remaining genera, it is fused with the nasal to form a nasopremaxillary. Characteristically the premaxillary of the *Amphibia* consists of three parts: the blade-like horizontal pars palatina, the dorsally directed pars facialis and the dentigerous pars dentalis which usually forms the edge of the jaw. In the *Apoda* the anatomy of this bone depends largely on the shape of the mouth. In *Ichthyophis* (P. and F. Sarasin, 1890) the lower jaw projects forward to more or less the same level as the upper jaw, and the premaxillary in this genus is normally developed: the pars palatina protects the anterior portion of the membranous floor of the nasal capsule, the pars facialis is applied to the anterior part of the medial wall of the cartilaginous nasal capsule, and the dentigerous pars dentalis forms the edge of the jaw. In most *Apoda*, however, the upper jaw projects far beyond the lower jaw, and in *Scolecomorphus* it projects so far that the anterior portion of the lower jaw does not reach the posterior portion of the premaxillary. In such genera, therefore,

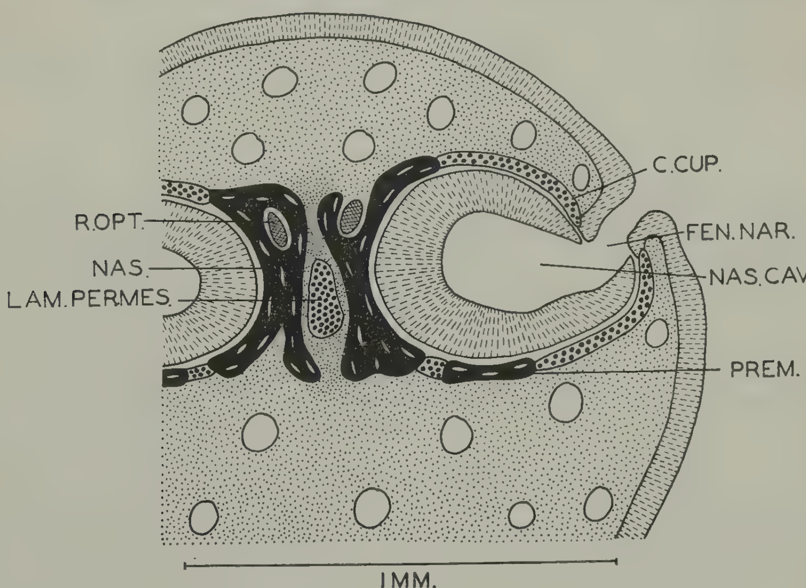

FIG. 5.

Transverse section through the anterior part of the nasal region.
C.CUP., cartilago cupularis; FEN.NAR., fenestra narina; LAM.PER.MES., lamina perpendicularis of the mesethmoid; NAS., nasal; NAS.CAV., nasal cavity; PREM., premaxillary; R.OPT., ramus ophthalmicus of the trigeminal nerve.

a relative backward shifting of the premaxillary has taken place, as a result of which the bone has a long and flat appearance (Fig. 2). The pars facialis appears in section lateral to the ventrally directed process of the nasal bone (Figs. 2 and 5). Its antero-lateral border is contiguous with the cartilago cupularis. Since the pars facialis is not directed dorsally as in *Ichthyophis*, the edge of the jaw is not as prominent as in the latter genus. The dentigerous pars dentalis stretches towards the middle line, but does not meet its partner. The pars palatina covers the anterior portion of the fenestra basalis nasi medial to the maxillopalatine. Posteriorly it overlaps the vomer ventrally. In all the remaining genera it forms a suture with the latter bone.

The large vomer behind the premaxillary covers the medial portion of the fenestra basalis nasi. Medially it is separated from its partner by connective tissue. In *Siphonops*, *Ichthyophis* and *Coecilia* (Wiedersheim, 1879) the vomers are suturally connected for nearly their whole length. In these genera there are also sutural connexions between the anterior border of the vomer and the premaxillary, whereas in *Scolecomorphus*, as previously mentioned, the two bones overlap. Anteriorly the medial edge of the vomer flanks the ventral edge of the lamina perpendicularis. Caudally the vomer becomes more or less U-shaped, and supports the medial portion of the nasal sac ventrally and ventro-laterally (Fig. 6). Further back the lamina horizontalis ventralis overlies the vomer dorso-medially. The posterior half of each vomer bears three backwardly directed teeth (Fig. 2). From this region it gradually tapers to a slender process terminating on the medial side of the choana. The vomerine canal, typical of all the *Apoda*, and situated within the dorsal portion of the bone, transmits the palatine nerve and a branch of the internal carotid artery.

Compared with the two bones previously described, the maxillopalatine is very large. Whereas the premaxillary forms the anterior part of the arch of the jaw, the maxillopalatine completes it laterally. In *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935) this bone is composed of the fused maxillary, palatine and lacrimal, and in some specimens also the pterygoid. In *Ichthyophis* (P. and F. Sarasin, 1890) it is composed of only the maxillary and the palatine. In *Coecilia*, *Siphonops* (Wiedersheim, 1879) and *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935) the maxillopalatine extends dorso-laterally and appears on the dorsal surface, where it forms a suture with the ventral portion of the nasopremaxillary and, behind this bone, with the vomer. In *Scolecomorphus*, owing to the presence of a prefrontal, the maxillopalatine is confined to a ventral position. There are no sutural connexions between it and the surrounding bones. It is separated from the prefrontal laterally and from the premaxillary and vomer medially by wide slit-like openings filled with connective tissue. Again, three portions can be distinguished in each maxillopalatine: the pars facialis, stretching dorso-laterally towards the latero-ventral edge of the prefrontal and syndesmotically attached to it; the pars palatina, which projects towards but does not reach the vomer; and the ventro-laterally directed, tooth-bearing pars dentalis (Fig. 6). In the anterior region of the nasal capsule, the dorsally directed pars facialis separates the nasal sac from the tentacle structure (Fig. 6), and is pierced by a foramen transmitting the two fused tentacle canals. The common tentacle canal opens into the anterior portion of the "Nebennase". Caudally the pars facialis becomes reduced to a short process, which in the choanal region projects dorso-medially and covers the choana dorso-laterally. The pars dentalis stretches caudally beyond the chaona. Its posterior part is firmly bound by connective tissue to the median anterior face of the squamosal (Fig. 2). In *Scolecomorphus* there is a wide gap between the posterior portion of the maxillopalatine and the basal bone, whereas in *Hypogeophis* (Marcus, Winsauer and Hueber, 1933) and *Siphonops* (Wiedersheim, 1879) the maxillopalatine

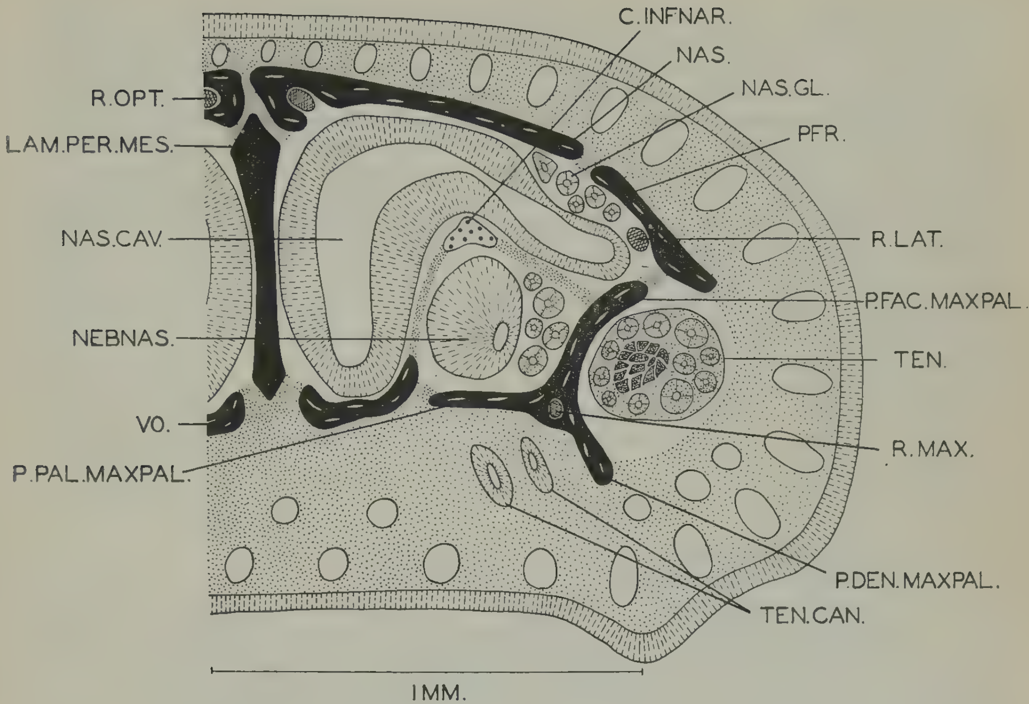

FIG. 6.
Transverse section through the nasal region.

C.INFNAR., cartilago infranarina; LAM.PER.MES., lamina perpendicularis of the mesethmoid; NAS., nasal; NAS. CAV., nasal cavity; NAS.GL., nasal gland; NEBNAS., nebennase; P.DEN MAXPAL., pars dentalis of the maxillopalatine; P.FAC. MAXPAL., pars facialis of the maxillopalatine; PFR., prefrontal; P.PAL.MAXPAL., pars palatina of the maxillopalatine; R.LAT., ramus lateralis nasi V(*a*); R.MAX., ramus maxillaris of the trigeminal nerve; R.OPT., ramus ophthalmicus of the trigeminal nerve; TEN., tentacle structure; TEN. CAN., tentacle canals; VO., vomer.

reaches the basal bone behind the choana and extends backwards to form the anterior border of the orbital opening. Although a small rudiment of the eye persists the orbital opening is completely absent.

The teeth of the maxillopalatine are arranged in two rows: the marginal teeth of the two maxillopalatines together with the premaxillary teeth form the outer tooth row; the vomerine teeth together with the medially and more posteriorly situated teeth of the maxillopalatines form the inner row (Fig. 2). The development of the maxillopalatine in *Scolecomorphus* is not known, but its inner posterior teeth undoubtedly belong to its palatina component as was shown to be the case in *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935). At least part of the medial posterior portion of the pars palatine must represent the palatine.

In the posterior part of the maxillopalatine the ramus maxillaris of the trigeminal nerve runs in the ventral groove between the pars palatina and the pars dentalis (Fig. 7). It then enters a canal in the maxillopalatine (Fig. 6), and subsequently emerges

through a foramen in its lateral face medial to the tentacle structure. The branches of this nerve innervate the skin on the lateral side of the snout.

On the antero-lateral side of the nasal capsule, in the gap between the dorsally situated nasal and the ventrally situated premaxillary, a small, roughly ellipsoidal bone with two anterior prongs, is present. This bone forms the posterior border of the fenestra narina and covers the anterior portion of the nasal sac laterally (Fig. 1). The dorsal prong lies in the space between the cartilago obliqua and the dorsally directed part of the cartilago infranarina (Fig. 3). It forms a small indentation in the lateral wall of the main nasal sac. The ventral prong is wedged in between the cartilago infranarina and the ventral posterior part of the cartilago cupularis (Figs. 2 and 4).

The bone has been described under various names: in *Ichthyophis* as nasale laterale (Wiedersheim, 1879) or as turbinale (P. and F. Sarasin, 1890); in *Uraeotyphlus* as turbinale (Peters, 1881); in *Scolecomorphus kirkii* as lachrymale (Peter, 1895) and in *Hypogeophis* as septomaxillare (Marcus, Stimmelmayr and Porsch, 1935). In the latter genus it is fused in the adult with the nasal and with the premaxillary to form a nasopremaxillary. According to Marcus, Stimmelmayr and Porsch (1935) this bone appears to be quite definitely a membrane bone. Judging from the descriptions

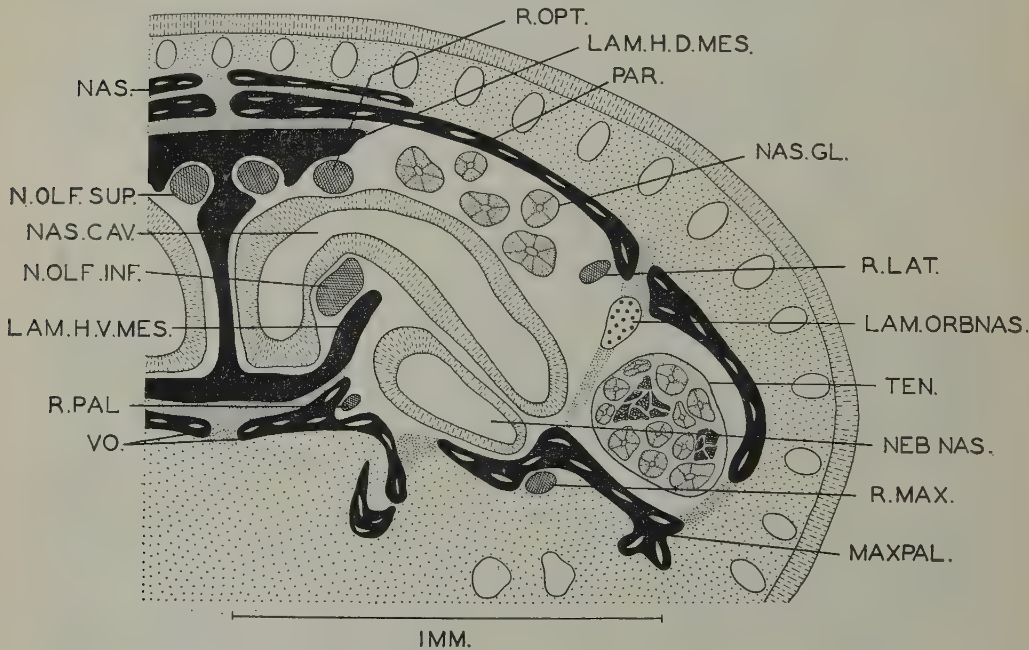

Fig. 7.

Transverse section through the posterior part of the nasal region.

LAM.H.D.MES., lamina horizontalis dorsalis of the mesethmoid; LAM.H.V.MES., lamina horizontalis ventralis of the mesethmoid; LAM.ORBNAS., lamina orbitonasalis; MAXPAL., maxillopalatine; NAS., nasal; NAS.CAV., nasal cavity; NAS.GL., nasal gland; NEBNAS., nebennase; N. OLF., INF., nervus olfactorius inferior; N. OLF. SUP., nervus olfactorius superior; PAR., parietal; R. LAT., ramus lateralis nasi V(*a*); R. OPT., ramus ophthalmicus of the trigeminal nerve; R. MAX., ramus maxillaris of the trigeminal nerve; R. PAL., ramus palatinus of the facial nerve; TEN., tentacle structure; VO., vomer.

available (Stadtmüller, 1936; Jarvik, 1942) it is undoubtedly homologous to the septomaxillary of the *Anura* and should be regarded as such in the *Apoda*. According to Stadtmüller (1936) it is also homologous to the septomaxillary of the *Urodela*. Jarvik (1942), however, agreeing with Lapage (1928) maintains that the septomaxillary of the *Urodela* is not a membrane bone as in the *Apoda* and *Anura*, but a cartilage bone. He suggested that this bone in the *Urodela* should be called a nariodal.

Immediately behind the septomaxillary the lateral wall of the nasal cavity is supported by the prefrontal (Fig. 1). It stretches beyond the choanal region, where its posterior portion is attached to the medial edge of the anterior part of the squamosal by connective tissue. At its posterior end the musculus adductor mandibulae externus major is attached to its ventral rim. Dorsally the prefrontal is separated from the nasal, and behind it from the frontal by connective tissue (Fig. 1). The prefrontal also occurs as a separate bone in *Ichthyophis* (P. and F. Sarasin, 1890), *Menotyphlus* (Stadtmüller, 1936) and *Uraeotyphlus* (Peters, 1881). In *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935) it is separate in the early stages, but fused with the frontal in the adult.

The greater part of the roof of the nasal cavity is formed by the nasal, which is a very large bony plate, the anterior portion of which, as already mentioned, projects ventrally (Fig. 2). Medially it is separated from its partner by connective tissue and posteriorly it overlaps the frontal.

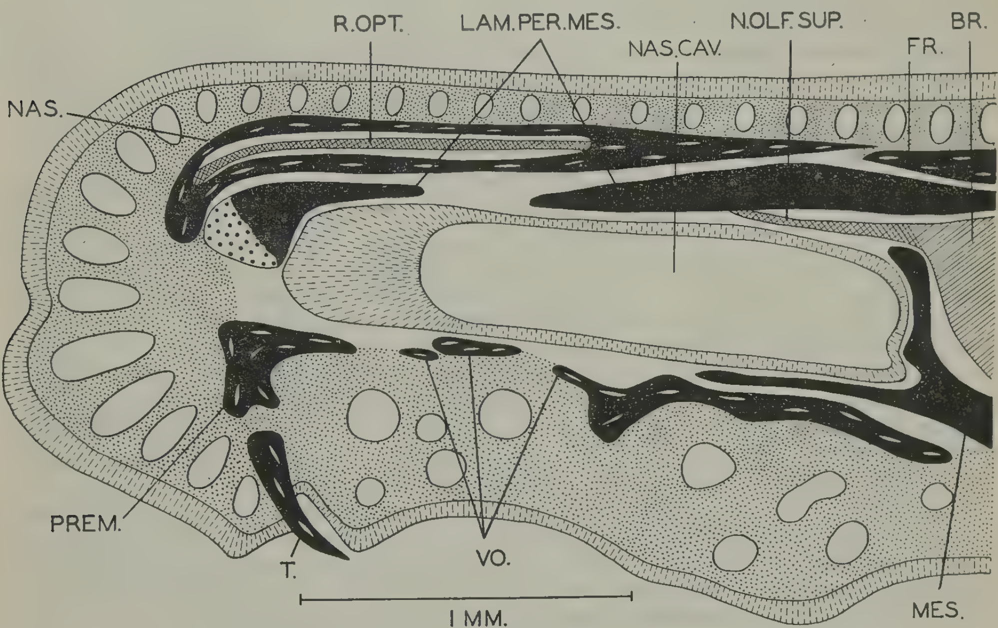

FIG. 8.

Sagittal section approximately through the median axis of the nasal region.

BR., brain; FR., frontal; LAM.PER.MES., lamina perpendicularis of the mesethmoid; MES., mesethmoid; N.OLF.SUP., nerus olfactorius superior; NAS., nasal; NAS.CAV., nasal cavity; PREM., premaxillary; R.OPT., ramus ophthalmicus of the trigeminal nerve; T., tooth; VO., vomer.

The large plate-like frontal covers the posterior portion of the nasal cavity. Medially it lies close to its partner in the mid-dorsal line. In *Boulengerula* (Peter, 1908) *Siphonops*, *Coecilia lumbricoides* (Wiedersheim, 1879) and *Dermophis* (de Jager, 1939) there is a wide gap between these bones with the result that the mesethmoid appears on the dorsal surface. Posteriorly the frontal ends in a short spike-like process, overlying the parietal laterally. Behind the prefrontal, the musculus adductor mandibulae externus major is attached to the ventral rim of this process.

It will have been seen that there are striking similarities between the nasal region of *Scolecomorphus* and that of *Ichthyophis* and *Uraeotyphlus*. All three genera have separate nasals, premaxillaries, septomaxillaries and prefrontals, with wide slit-like openings separating the individual bones from one another. These characteristics led Sarasin (1890) to believe that *Ichthyophis* and *Uraeotyphlus* are closely related to the *Urodela* and that they form the link between the latter and the remaining *Apoda*. Peter (1895) considered them the most primitive of the *Apoda*, but de Villiers (1938) pointed out that these features are the reverse of primitive and should be considered indicative of degeneration or perhaps of neoteny.

THE ORBITOTEMPORAL, OTIC AND OCCIPITAL REGIONS

The bones of the orbitotemporal, otic and occipital regions are so closely fused that the floor and side-walls of the brain-case are formed almost entirely by a single compound bone, termed by Sarasin (1890) the os basale. The development of this bone has been studied with the help of wax models in *Ichthyophis* (Sarasin, 1890; Peter, 1898) and *Hypogeophis* (Marcus, Winsauer and Hueber, 1933; Marcus, Stimmelmayr and Porsch, 1935). In the early stages of *Hypogeophis* Marcus and his students were able to trace a large number of separate centres of ossification. According to their findings the basal is composed of the fused bones of the otic capsule as well as the parasphenoid, pleurosphenoids, basioccipital, supraoccipital and exoccipitals. The composition of this structure in the adult *Scolecomorphus* is very similar to that of *Hypogeophis*, and it is quite possible that most of the separate centres of ossification found in *Hypogeophis* are also present in the early stages of *Scolecomorphus*, a point which could, however, only be cleared up by studying the ontogeny of the structures in question.

In the orbitotemporal region the only bone which can be definitely identified is the orbitosphenoid. It forms the anterior portion of the side-wall of the brain-case and extends from the posterior border of the lamina orbitonasalis to the optic foramen which it borders anteriorly. It is fused anteriorly with the posterior border of the lamina praecerebralis of the mesethmoid. Behind the optic foramen the components of the lateral wall of the brain-case are fused throughout the orbitotemporal, otic and occipital regions as part of the os basale. Immediately in front of the otic capsule the side-wall is perforated by the large trigeminal foramen. The ganglion Gasseri is situated in the foramen and through it pass the branches of the trigeminal and abducent nerves and the vena capitis lateralis.

The portion of the os basale which forms the lateral wall of the brain-case between the optic foramen and the trigeminal foramen is similar to that of *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935) and presumably corresponds to the pleurosphenoid of the latter genus. Between the anterior portion of this bone and the posterior end of the orbitosphenoid there are two strips of cartilage, the one below and the other above the optic foramen (Fig. 2). In *Hypogeophis*, according to Marcus,

Stimmelmayr and Porsch (1935) these strips of cartilage represent residual portions of the trabecula and of the taenia marginalis respectively.

On its ventro-lateral aspect, slightly behind the foramen for the trigeminal and abducent nerves, the basal bears a large cartilaginous basipterygoid process (Fig. 9). According to some authors, the process has a very definite relationship to the position of the foramen for the palatine branch of the facial nerve. De Beer (1926, p. 311) makes the following statement for *Apoda*: "There is a true basitrabecular process, behind which passes the palatine nerve, enclosed in a foramen formed by an extension of the subocular shelf . . ." This statement does not, however, apply to all genera. Marcus, Stimmelmayr and Porsch (1935) found that in some genera this foramen is situated in front of, and in others behind, the basipterygoid process. In *Scolecomorphus* the ramus palatinus leaves the cranial cavity more or less opposite the middle of the basipterygoid process and enters a canal within the basal bone. It continues rostrad in this canal and is accompanied by a branch of the internal carotid artery. In front of the basipterygoid process these structures emerge from this canal and continue together to the anterior region of the skull.

The medial wall of the otic capsule is perforated by several foramina. De Villiers (1938) observed three foramina transmitting the ramus anterior, ramus medianus and the ramus posterior of the n. acusticus. Judging from my specimen it is evident that the number of foramina is subject to variation. On the left side there are five, and on the right side four, foramina acustica. The two anterior foramina of the right side are situated ventrally in the anterior portion of the medial wall. Dorsally to the second of these foramina the medial wall is pierced by the large foramen endolymphaticum and further back, but more ventrally by the foramen perilymphaticum. Between the foramen endolymphaticum and the foramen perilymphaticum two more foramina acustica are present. The foramina on the left side are similar to those on the right, except that there is a small fifth foramen in a position halfway between the corresponding first two of the right side. The lateral wall of the otic capsule is complete, whereas in all the remaining genera hitherto described it is pierced by the large fenestra ovalis.

In front of the optic foramina the portion of the basal bone which forms the floor of the cranial cavity is more or less wedge-shaped. It extends anteriorly into the nasal region where it tapers to a sharp point, ending dorsal to the vomers (Fig. 2). Its lateral edge is separated from the orbitosphenoid by connective tissue. In the region behind the optic foramen it is indistinguishably fused with the side-wall of the braincase. Similar conditions obtain in *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935) where the ontogeny shows that this portion of the os basale represents the parasphenoid.

In the occipital region of *Hypogeophis* Marcus, Stimmelmayr and Porsch (1935) found the basioccipital, exoccipitals and supraoccipital to be separate in the early stages. In later stages, however, the basioccipital fuses with the posterior border of the parasphenoid and together these two bones form the entire floor of the braincase. Laterally the basioccipital fuses with the exoccipital, which in turn fuses anteriorly with the posterior portion of the otic capsule. Postero-dorsally the two exoccipitals are united with each other across the midline by the supraoccipital. In the adult stage the bones of the occipital region are therefore completely fused with one another and also with the rest of the basal bone, thus forming a ring around the posterior portion of the cranial cavity. All the *Apoda* in which the development of the skull has been investigated, agree in lacking both a tectum synoticum and a tectum posterius. The *Apoda*, like all the other living and most extinct *Amphibia*, cannot therefore have a

genuine supraoccipital. Since the bone which Marcus and his co-workers describe as a supraoccipital arises as a membrane bone, its homology with a true supraoccipital cannot be accepted.

In *Ichthyophis* (Peter, 1898) only two separate centres of ossification are present in the occipital region: a ventrally situated basioccipital ("Occipital-platte") and a laterally situated exoccipital (Occipitale laterale). In the adult stage of this genus the basioccipital is fused anteriorly with the parasphenoid and laterally with the exoccipitals. The exoccipital is also fused with the posterior portion of the otic capsule. Dorsally it stretches towards the mid-dorsal line where it is suturally connected with its partner from the opposite side. A "supraoccipital" as found in *Hypogeophis* (Marcus, Stimmelmayr and Porsch, 1935) is absent. In *Scolecomorphus* this region is very similar to that of *Ichthyophis*. The dorsal portions of the os basale which presumably correspond to the exoccipitals of *Ichthyophis* are, however, separated from each other by connective tissue and are not suturally joined as in *Ichthyophis*. Postero-dorsally the brain-case has no bony roof, since the dorsal portions of the presumed exoccipitals do not reach as far as the posterior end of the skull (Fig. 1).

The anterior portion of the roof of the cranial cavity is formed by the large, plate-like frontals, which, as already mentioned, also cover the posterior parts of the nasal cavities. Behind the frontals the roof of the brain-case is formed by the extensive parietals. Anteriorly they are overlapped by the frontals and medially they are separated from each other by connective tissue. Posteriorly they reach as far as the posterior end of the otic region. Behind the parietals the dorsal portions of the basal bone, presumably representing the exoccipitals, complete the roof of the skull.

In *Siphonops annulatus* (Wiedersheim, 1879) and *Hypogeophis alternans* (Marcus, Stimmelmayr and Porsch, 1935), the medial edge of the squamosal is contiguous to the lateral edge of the parietal and consequently these two species are stegokrotaphic. In *Hypogeophis* the squamosal is a compound bone: its anterior portion which borders the orbital opening dorsally, posteriorly and ventrally, in reality represents the postorbital (Marcus, Stimmelmayr and Porsch, 1935). In *Coecilia rostrata*, *Coecilia lumbricoides* (Wiedersheim, 1879) and *Dermophis gregorii* (de Jager, 1940) the squamosal and the parietal are separated by a narrow slit. These species are, therefore, slightly zygokrotaphic. In all of them, the anterior portion of the squamosal, presumably representing the postorbital, borders the orbital opening dorsally, posteriorly and ventrally as in *Hypogeophis*. In *Ichthyophis glutinosus* (Wiedersheim, 1879), another slightly zygokrotaphic species, the postorbital remains as a separate bone in the adult stage and borders the orbital opening as in *Hypogeophis*. In *Siphonops indistinctus* (Wiedersheim, 1879), a much more zygokrotaphic species, the anterior portion of the squamosal still borders the orbital opening posteriorly, and separates it from the large temporal fossa. In *Scolecomorphus* the temporal fossa is much larger than that of any other *Apoda* hitherto described. The anterior part of the squamosal, comparable with the postorbital of *Hypogeophis*, is so greatly reduced that only a slender portion of the bone remains in this region (Fig. 1). It is attached anteriorly to the lateral edge of the posterior end of the prefrontal. As a result of this reduction of the squamosal and probable disappearance of the postorbital, the orbital opening becomes confluent with the temporal fossa as in birds.

Posteriorly the squamosal stretches into the suspensorial region where it is firmly attached by connective tissue to the dorso-lateral face of the palatoquadrate (Fig. 9).

According to Goodrich (1930) stegokrotaphy in *Apoda* is probably due to secondary consolidation and not to the survival of the stegocephalian roof. On the

other hand, Marcus, Stimmelmayr and Porsch (1935), and de Villiers (1938) consider the skull of the *Apoda* as primarily stegokrotaphic. De Villiers (1938, p. 2) in fact, considers the *Apoda* " . . . the most stegocephaline of all the existing *Amphibia*". According to him zygokrotaphy must be regarded as a result of degeneration in the *Apoda*.

THE PALATOQUADRATE AND SUSPENSORIAL REGION

The extensively ossified pars quadrata palatoquadrati is situated antero-lateral to the otic capsule. As in most *Apoda*, the basipterygoid process is long, so that the

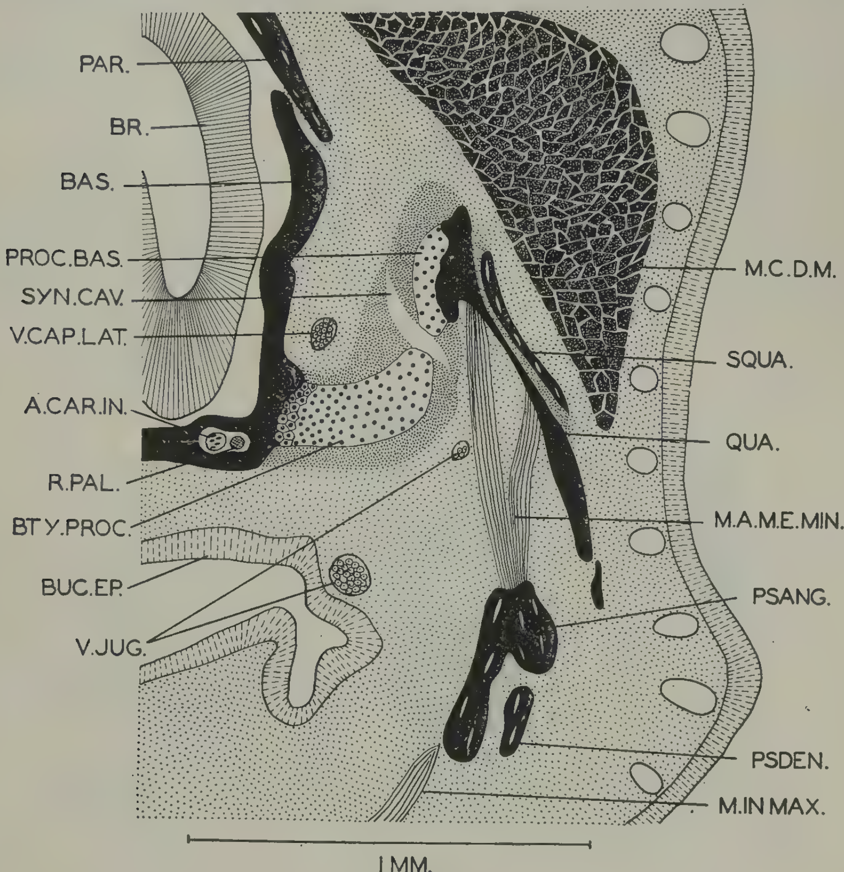

FIG. 9.

Transverse section through the suspensorial region.

A.CAR.IN., arteria carotis interna; BAS., basal bone; BTY.PROC., basipterygoid process; BR., brain; BUC.EP., buccal epithelium; M.A.M.E.MIN., musculus adductor mandibulae externus minor; M.C.D.M., musculus cephalo-dorso-maxillaris; M.INMAX., musculus intermaxillaris; PAR., parietal; PROC.BAS., processus basalis; PSANG., pseudo-angular; PSDEN., pseudodentary; QUA., quadrate; R.PAL., ramus palatinus of the facial nerve; SQUA., squamosal; SYN.CAV., synovial cavity; V.CAP.LAT., vena capitis lateralis; V.JUG., vena jugularis.

palatoquadrate is situated far out to the side of the skull. Through the wide cranio-quadrate passage pass the rostradly directed branch of the a. carotis interna, the vena capitis lateralis and the vena jugularis. In *Coecilia* (Wiedersheim, 1879) the quadrate lies close to the brain-case and the cranio-quadrate passage is almost obliterated.

In most genera the pars quadrata has several processes. In *Ichthyophis*, Peter (1898) describes a small processus oticus projecting from the posterior part of the bone towards the anterior edge of the otic capsule. Goodrich (1930) describes a similar process in *Siphonops*, in which it establishes contact with the otic capsule. In *Hypogeophis*, Marcus, Stimmelmayr and Porsch (1935) also mention a slight posterior projection of the quadrate but they do not homologize it with a processus oticus. In *Scolecomorphus* this process is absent.

Medially the palatoquadrate bears a well-developed processus basalis, which articulates with the basipterygoid process of the basal bone. A connective tissue capsule and synovial cavity are present (Fig. 9). Similar conditions obtain in *Hypogeophis* (Marcus, Winsauer and Hueber, 1933) and *Dermophis* (de Jager, 1939). In *Coecilia* (de Jager, 1940) these two processes have fused so closely that the articulation in this genus is in the process of being lost. In the adult *Ichthyophis* (Peter, 1898) the palato-quadratobasal articulation is replaced by fibrous tissue.

There is no processus ascendens palatoquadrati. In *Hypogeophis* (Marcus, Winsauer and Hueber, 1933), *Ichthyophis* (Peter, 1898) and *Siphonops* (Edgeworth, 1925) this process is well developed. In the latter genus it is continuous with the taenia marginalis, while in *Hypogeophis* and *Ichthyophis* it is syndesmotically attached to it.

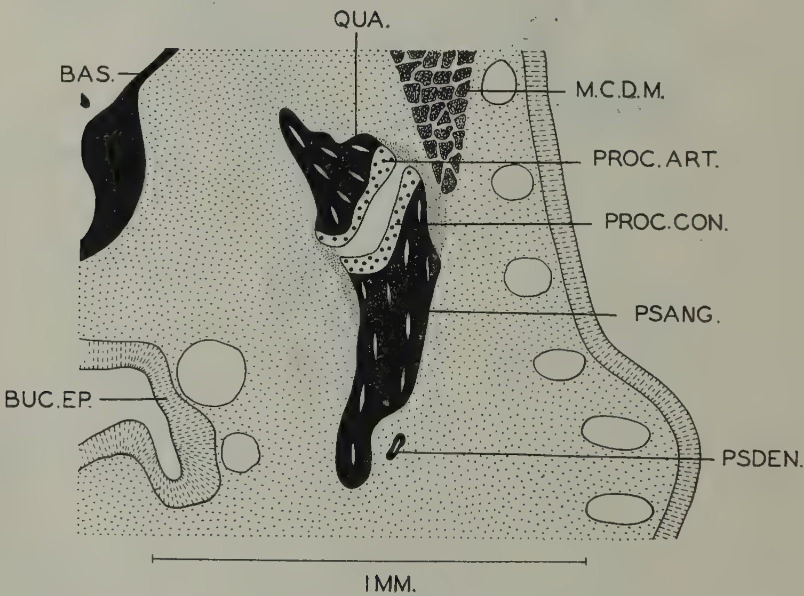

Fig. 10.

Transverse section to show the articulation between the palatoquadrate and the lower jaw.

BAS., basal bone; BUC.EP., buccal epithelium; M.C.D.M., musculus cephalo-dorso-maxillaris; PROC.ART., processus articularis; PSANG., pseudo-angular; PSDEN., pseudodentary; PROC. CON., processus condyloideus; QUA., quadrate.

Posteriorly the quadrate bears a processus articularis for articulation with the lower jaw (Fig. 10). In *Ichthyophis* (Peter, 1898), *Siphonops* (Wiedersheim, 1879) and *Hypogeophis* (Marcus, Winsauer and Hueber, 1933) the palatoquadrate also bears a well-developed processus columellaris for articulation with the stapes. According to de Jager (1940) there is some fusion of the articular surface of the processus columellaris and that of the stapes in most of the remaining genera. In *Scolecomorphus*, the stapes as well as the processus columellaris is absent.

Anteriorly the quadrate bears two short processes (Fig. 2). Both of these are firmly attached by connective tissue to the squamosal. The more medially situated of these processes probably represents the reduced pterygoid fused with the quadrate. In *Ichthyophis*, *Coecilia* and *Siphonops* (Luther, 1914) the pterygoid occurs as a separate bone. In *Hypogeophis*, Marcus, Stimmelmayr and Porsch (1935) found the pterygoid to be separate in some specimens, while in others it is incorporated in the maxillopalatine or in the processus pterygoideus palatoquadrati.

The more laterally situated process is almost certainly the quadratojugal (quadratomaxillary). De Villiers (1936) furnishes ontogenetical evidence that a similar process of the quadrate in *Hypogeophis* arises as a separate bone which could only be the quadratojugal. On comparative anatomical grounds he concludes that an anteriorly directed process of the quadrate in *Boulengerula* likewise represents the quadratojugal.

The muscles associated with the suspensorial region have been fully described by Luther (1914) for *Ichthyophis*, *Coecilia* and *Siphonops*, and by de Villiers (1938) for *Scolecomorphus* and *Boulengerula*. For a detailed account the reader is referred to the works of these authors. The following is a concise account of the conditions obtaining in my specimen: The m. adductor mandibulae externus major is very large and, as previously described, arises from the parietal, prefrontal and frontal. Ventrally it inserts on the dorsal surface of the lower jaw. The m. adductor mandibulae externus minor arises partly from the squamosal and partly from the pterygoquadrate. Ventrally it inserts on the lower jaw immediately behind the insertion of the m. adductor mandibulae externus major. The m. pseudo-temporalis described by Luther (1914) for *Coecilia*, *Ichthyophis* and *Siphonops* is absent. The m. pterygoideus arises from the ventral surface of the processus pterygoideus palatoquadrati and inserts on the medial surface of the lower jaw. The large, longitudinally disposed m. cephalo-dorso-maxillaris arises together with the m. adductor mandibulae externus major from the lateral edge of the parietal. The m. levator quadrati is absent.

Turning now to the movement of the palatoquadrate one finds that:

(1) The quadrato-stapedial articulation is absent.

(2) The m. levator quadrati which, in other genera, is responsible for the movement of the pterygo-quadrate against the basal bone, is absent.

(3) The palato-quadrate is firmly applied to the squamosal by connective tissue, and no movement seems possible between these two bones.

It is therefore quite evident that the skull is monimostylic, a conclusion also arrived at by de Villiers (1938) for the same species. The absence of the quadrato-stapedial articulation and of the m. levator quadrati is apparently unique among *Apoda* and must be regarded as a secondary feature owing to degeneration or possibly neoteny.

According to Eifertinger (1933), who made a thorough study of the structure and development of the lower jaw of *Hypogeophis*, nine individual bones: the dentary, splenial, coronoid, supra-angular, mentomeckelian, angular, pre-articular, articular and complimentale are laid down in the embryo. In the adult the first five of these are fused into a single compound bone, the pseudodentary, and the last four are similarly fused to form the pseudoangular. In *Scolecomorphus* the lower jaw consists of only two bones, and judging by their structure and mutual relationships they are homologous with the pseudodentary and pseudoangular of *Hypogeophis*.

The symphysis between the anterior tips of the pseudodentaries is formed by fibrocartilage. The mental symphysis in *Coecilia*, *Ichthyophis* and *Siphonops* (Wiedersheim, 1879) is apparently of the same nature. Anteriorly the dorsal surface of the pseudodentary is deeply grooved; its outer rim, presumably the portion which represents the dentary, bears a single row of teeth (Fig. 11). Posteriorly the bone gradually flattens and tapers towards the articular region.

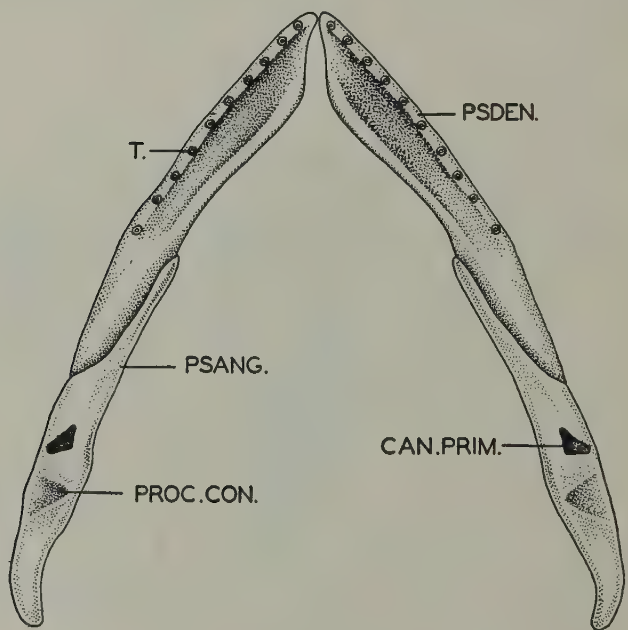

Fig. 11.

Graphic reconstruction of the lower jaw × 22·2. Dorsal view.

CAN.PRIM., canalis primordialis; PROC.CON., processus condyloideus; PSANG., pseudo-angular; PSDEN., pseudodentary; T., tooth.

The anterior portion of the pseudo-angular is applied to the medial surface of the posterior part of the pseudodentary, and reaches forward to the level of the last tooth (Fig. 11). In the sulcus primordialis, between the apposed surfaces of these bones lies a slender cartilaginous rod representing the reduced Meckels cartilage. The anterior tip of the latter is perichondrally ossified for a short distance and must represent the posterior extremity of the mentomeckelian, which has become incorporated in the pseudodentary. Its posterior portion is ossified as the articular, which is fused with the lateral edge of the pseudoangular.

The large, pyramid-shaped processus internus of the pseudoangular for the insertion of the m. adductor mandibulae externus major in *Hypogeophis* (Eifertinger, 1933), is absent in *Scolecomorphus*. In the latter this muscle is inserted on the dorsal surface of the pseudoangular. Upon leaving the ganglion Gasseri, the raumus mandibularis runs ventro-laterally and enters the sulcus primordialis through the canalis primordialis (Fig. 11); it gives off various branches to the skin of the lower jaw. In *Hypogeophis*, the chorda tympani pierces the pseudoangular through a separate foramen; in *Scolecomorphus* this nerve is absent.

The well-developed processus condyloideus is situated on the postero-dorsal surface of the pseudoangular, slightly behind the canalis primordialis.

HYOBRANCHIAL APPARATUS

Our knowledge of the hyobranchial apparatus of the *Apoda* is practically limited to work on *Ichthyophis* (Wiedersheim, 1879; Sarasin, 1890 and Peter, 1898).

The apparatus is best understood from an inspection of the graphic reconstruction (Fig. 12). It consists of an anteriorly situated hyoid arch and four branchial arches lying one behind the other. The hyoid arches and the first pair of branchial arches are connected medially by means of what is, in comparison with the condition in *Ichthyophis*, a very short copula. The second pair of branchial arches is isolated from the rest of this apparatus, but medially they are fused with each other. The fourth pair differs from the others in that the arches are not connected anteriorly in the medial line, but each arch is fused with the medial side of the third branchial arch, mid-way along its course. The fourth branchial arch, overlooked by Wiedersheim (1879), was described in *Ichthyophis* by P. and F. Sarasin (1890). In this genus, however, it is very short and rudimentary, whereas in *Scolecomorphus* it consists of a broad flat cartilaginous plate, extending far back, and fusing posteriorly with its counterpart above the larynx.

For the larval stages of *Ichthyophis* Peter (1898) pointed out that the rudimentary fourth branchial arch is separate from the third, but is fused with it in the

adult. The Sarasins (1890) found two copulae present in the larval stage of *Ichthyopis*, the first between the hyoid arches and the first pair of branchial arches, and the other between the first and the second pairs of branchial arches. The second copula disappears entirely in the adult stage.

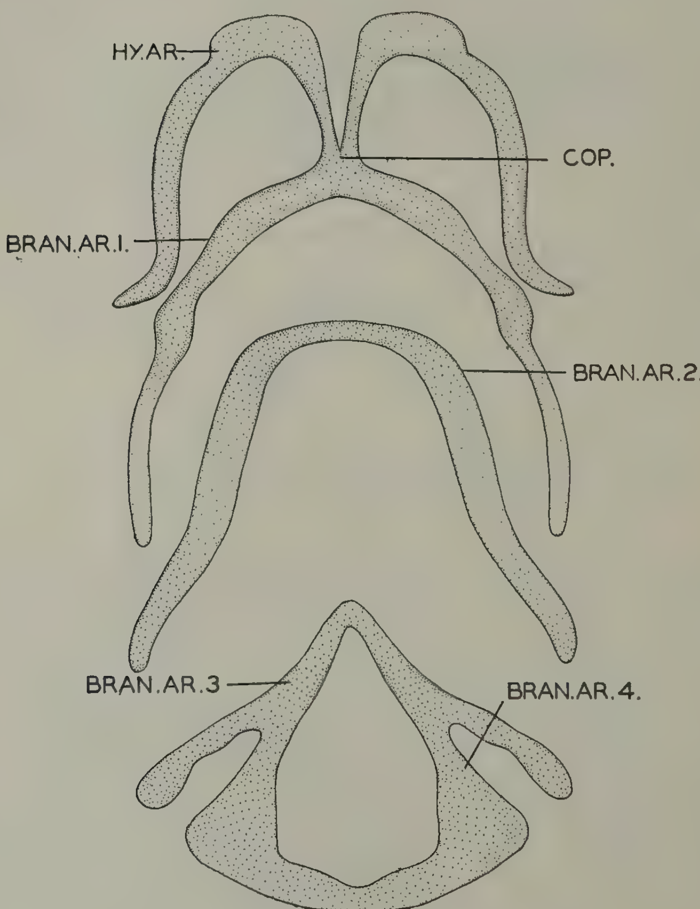

FIG. 12.

Graphic reconstruction of the hyobranchial apparatus × 22·2. Dorsal view.

BRAN.AR.1, branchial arch 1; BRAN.AR.2, branchial arch 2; BRAN.AR.3, branchial arch 3; BRAN.AR.4, branchial arch 4; COP., copula; HY.AR., hyoid arch.

SUMMARY

1 The lateral wall of the nasal capsule is incomplete.
2 The fenestra narina lacks a posterior border.
3 The cartilago infranarina forms a ventral indentation in the main nasal sac thus giving it a semilunar shape.
4 The processus praenasalis medius inferior is absent.
5 The foramen apicale and the foramen epiphaniale are absent.
6 The nasals, premaxillaries, septomaxillaries and prefrontals are separate.
7 The upper jaw projects far beyond the lower, and a relative backward shifting of the premaxillary has taken place.
8 The bones of the orbitotemporal, otic and occipital regions are fused to form a single compound bone, the os basale.
9 The basipterygoid process is well-developed.
10 The ramus palatinus leaves the cranial cavity more or less opposite the middle of the basipterygoid process and not behind it.
11 The number of foramina acustica is subject to variation not only within the same species but also on the left and right sides of the same specimen.
12 The fenestra ovalis is absent.
13 The tectum synoticum and the tectum posterior are absent.
14 *Scolecomorphus* is zygokrotaphic.
15 The postorbital is apparently absent, and the orbital opening is confluent with the temporal fossa.
16 The processus basalis palatoquadrati is well-developed.
17 The processus oticus, the processus ascendens and the processus columellaris are absent.
18 The stapes is absent.
19 The m. pseudo-temporalis and the m. levator quadrati are absent.
20 The skull is monimostylic.
21 In the adult, the lower jaw consists of only two bones, the pseudodentary and the pseudoangular.
22 The symphysis between the anterior tips of the pseudodentaries is formed by fibrocartilage.
23 The chorda tympani is absent.
24 The hyobranchial apparatus consists of a hyoid arch and four well-developed branchial arches.
25 The copula is very short.

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